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THE ENVIRONMENTAL FACTORS IN THE DISTRIBUTION OF ANIMALS

By Alexander G. Ruthven
University of Michigan

It is now recognized that American students of zoögeography are sharply divided into two schools on the interpretation of the distribution of the North American fauna. One group holds to the life-zone theory, with its fundamental tenet that the fauna and flora are grouped into transcontinental zones by the effect of temperature, the northward distribution of terrestrial animals and plants being governed by the sum of the positive temperatures for the entire season of growth and reproduction, the southward distribution by the mean temperature of a brief period during the hottest part of the year.[1] The other, and much the smaller, group believes that the facts of distribution do not indicate zonal distribution and that the facts of physiology and ecology do not warrant the expectation that given intensities of any one environmental factor will be found to exert a predominating influence upon the distribution of faunas.

It should be recognized that this difference of opinion and viewpoint at least augurs well for the advancement of our knowledge of the geographic factors; for, while it is well to draft theories on the basis of available facts, it is equally desirable that these theories be subjected to a most searching criticism. Unfortunately, there is reason to believe that among the students who have adopted the life-zone theory there are those who are considering as absolute truth that which is merely the accepted, and possibly erroneous, belief predominant at the present time and others who are unduly impressed by the fact that the theory has been adopted by an active and important government bureau.

Circumstances Giving Support to the Life-Zone Theory

There are other reasons, however, for the wide acceptance which the theory enjoys. Analysis of the geographic factors is proceeding very slowly; distribution of individual species is often limited to the north and south or connected with altitude in a way that suggests temperature control; temperature and other climatic conditions are important physiological agents and vary in a rather definite way with latitude, longitude, and altitude; data on the facts of distribution are still very limited; and the methods employed by advocates of the life-zone theory yield results which apparently confirm the theory. It need not be argued that the objections to the theory, which concern both the facts and their interpretation, should not be lost sight of but may with propriety be emphasized and reiterated until satisfactorily met.

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[1] C. Hart Merriam: Life Zones and Crop Zones of the United States, *U. S. Dept. of Agric. Biological Survey Bull. No. 10*, Washington, D. C., 1898, p. 54.

OBJECTIONS TO THE LIFE-ZONE THEORY

Briefly stated, some of these objections are that the distribution of species apparently does not correspond to the accepted life zones as often or as nicely as would be expected; ecological studies yield an increasing amount of evidence that environmental factors other than the climatic ones may play an important rôle in distribution; and the data of physiology lead to the conclusion that a change in any environmental factor may make living conditions impossible. If these objections cannot be answered, the life-zone theory can continue to be held only by those who fail to resist the appeal of a dogmatism supported by extraordinary authority but largely based upon facts to which it is unrelated.

As has been intimated, there is an apparent zonal distribution of animals. It is a matter of common observation that as one ascends high mountains or journeys across the country from north to south or in the opposite direction certain species of plants and animals give way to others, and because the ranges of several conspicuous forms are frequently interrupted at about the same places it is the practice to consider the intervening area as a faunal region or zone. It is pertinent to inquire, however, whether the zones may not apply principally to the conspicuous forms; or, more broadly, one may ask what proportion of the organisms reacts to the changing conditions at the zonal boundaries.

DIFFERENT RANGES IN THE SAME AREA

Very little study is needed to reveal the fact that the forms in the same area usually have different distributions; that is in a given region many species or subspecies fall short of, or exceed, the ranges of the conspicuous forms which serve as an index to the zones. It is not necessary to give specific examples, since the statement will not be controverted. Indeed it is definitely admitted in at least one report based on the life-zone theory, for, referring to the distribution of Texas animals, Bailey[2] states: "It [the Lower Sonoran Zone] is characterized by the following species, some of which fill the subdivision and are restricted to it, while many more are restricted to definite areas within its limits, and still others range beyond through one or more of the other zones."

It is believed that when the entire fauna is considered almost every region will appear as a transition area, the fauna being composed of three elements; forms which do not range beyond the area in a given direction, forms which do not range beyond it in the opposite direction, and forms

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[2] Vernon Bailey: Biological Survey of Texas, *North American Fauna No. 25*, Biological Survey, U. S. Dept. of Agric., Washington, D. C., 1905, p. 26.

DISTRIBUTION OF LIZARDS AND SNAKES, DAVIS MOUNTAINS REGION, TEXAS

Altitudinal Distribution	SPECIES (Italicized forms rare or secretive in the region)	TOTAL NUMBER of SPECIES 33	MORE COMMON FORMS IN	
			WESTERN TEXAS 24	TEXAS 25
Confined to lowlands below 3,600 feet on north (Lower Sonoran zone)	Cnemidophorus tessellatus tessellatus *Leptotyphlops dulcis* *Elaphe subocularis* *Elaphe laeta* *Lampropeltis splendida* *Ficimia cana* *Hypsiglena ochrorhynchus texana* Natrix sipedon transversa (a) Thamnophis proximus (a)	9	3	3 or 12%
Confined to mountains above 4,200 feet on north (Upper Sonoran zone)	Uta ornata (b) Plestiodon brevilineatus (b) *Plestiodon guttulatus* *Salvadora grahamiae* *Heterodon nasicus* (c) Thamnophis eques (b) Crotalus molossus	7	4	1 or 4%
Common to lowlands and mountains—both zones (*known to occur at least as high as 5,000-5,800 feet)	Coleonyx brevis *Holbrookia maculata maculata (d) *Holbrookia texana *Crotaphytus collaris baileyi (e) *Sceloporus torquatus poinsettii (e) *Sceloporus consobrinus consobrinus *Phrynosoma cornutum *Phrynosoma modestum *Cnemidophorus grahamii *Cnemidophorus sexlineatus *Cnemidophorus gularis *Coluber flagellum flagellum *Coluber taeniatus girardi *Thamnophis marcianus *Pituophis sayi Crotalus atrox *Crotalus lepidus (d)	17	17	21 or 84%

(a) Conspicuous habitat preference (semi-aquatic forms).

(b) Found in Lower Sonoran zone elsewhere in Texas (J. K. Strecker: Contributions to Texan Herpetology, *Baylor Univ. Bull.*, Vol. 12, No. 1, Waco, 1909).

(c) Recorded as occurring in Lower Sonoran zone in Texas (Bailey: Biological Survey of Texas, *North Amer. Fauna No. 25*).

(d) Recorded as occurring in Lower Sonoran zone in western Texas (Bailey, *op. cit.*).

(e) Conspicuous habitat preference (saxicolous forms).

which range beyond it in both directions. This general fact is concealed or its importance minimized by advocates of the life-zone theory by the practice of listing the species by zones. Yet it cannot be ignored, for to characterize zones by forms which do not approach their boundaries, or which exceed their limits, certainly does not throw light upon the authenticity of the divisions.

Need of Critical Distributional Studies

It is necessary to show that the zones express, at least with reasonable accuracy, the ranges of an unusual number of forms, if they are to have significance relative to the fauna as a whole. Unfortunately, but little attention has been given to conditions in the critical areas at the boundaries of contiguous zones, but at least it has not been shown definitely that a large part of the fauna of what are transition regions in the life-zone classification reacts to the particular changes in the one condition which is supposed to mark the common boundary of zones. As a contribution to this problem the writer offers the results of a critical study of the distribution of the lizards and snakes on the northern side of the Davis Mountains, Texas, where there are, according to the United States Biological Survey, two zones, Lower Sonoran and Upper Sonoran.

A Distributional Study from the Davis Mountains, Texas

In analyzing the facts of distribution set forth in this table it should be recognized, although this is not generally done, that the rare or secretive species are not significant and that their presence in statistical summaries is misleading and increases the chances of error already great enough from lack of data. The table shows that of the more common forms less than 30 per cent appear to be peculiar to particular zones if our knowledge of the distribution of the forms in western Texas is alone considered, and but 16 per cent if data on the distribution in a wider area are admitted. That is the ranges of only 16 per cent of the forms are limited in the region of the common boundary of the zones.

The arrangement of the forms in the table cannot be attacked on the ground that zonal boundaries are not exact and that the list of forms common to both zones has been increased by the inclusion of forms which only enter the lower part of the Upper Sonoran zone or the opposite, for a transition zone of 600 feet has been allowed. All of the species found in both areas are wide-ranging forms on the lowlands, and at least fifteen of the seventeen forms found in both zones have been found at the high elevations in the Upper Sonoran zone of 5,000–5,800 feet. It is admitted that the information is not complete because much is yet to be learned about the fauna, but it may be pointed out that life zones have been mapped for most regions on relatively less data than those used in this study, and, as the list of species evidently represents practically all of the common forms of the region, there is no reason to believe that a greater response on the part of the fauna to the differences in conditions between the two zones will be discovered.

Any consideration of the possible factors in zoögeography must now take cognizance of the increasing amount of data which show that environmental factors other than the climatic ones control distribution and may even cause apparent zonal distribution of some forms. Thus Newman and Patterson[3] have found that soil controls the local distribution of the lizard *Sceloporus spinosus floridanus* in a region in Texas, and the writer has shown that the presence of rocks on the mountains and of fine soil in the valleys causes a differentiation in the distribution of several reptiles in Nevada into mountain forms and plain forms.[4]

It is admitted that when the ranges of a number of forms are limited at a certain place climatic factors may be the operative ones, but it is claimed that data on distribution are not sufficient to establish this fact. On the other hand, it is sometimes possible to demonstrate the occurrence of other geographic factors from the data of distribution, particularly if animals found in two zones but having a principal distribution in one region or the other are selected. The conditions in the Davis Mountains region (southwestern Texas) illustrate this point.

ECOLOGICAL FACTORS AS A DISTRIBUTIONAL CONTROL IN THE DAVIS MOUNTAINS

Two of the species found in both zones (*Crotaphytus collaris baileyi* and *Sceloporus torquatus poinsettii*) are distinctly saxicolous in habits. These forms are common in the mountains but so rare on the adjacent hills and plains as to be easily overlooked. That climatic factors have little to do with this distribution, however, is clearly indicated by the fact that the species are relatively abundant on the plains in the few places where there are large rocks or small rock exposures. In other words the difference in the abundance of these species on the mountains and plains is evidently due to their choice of habitat and to the fact that the rocks have been largely destroyed or buried in the region adjacent to the mountains. It is also suggestive that *Crotaphytus collaris baileyi*, which is less of a rock climbing form but commonly lives beneath rocks, is more abundant and widely distributed on the plains than is *Sceloporus torquatus poinsettii* which is a strictly scansorial form. This would be expected from the difference in habits, since loose rocks are found later than cliffs in such a geographic change. It is not too much to expect that other less saxicolous mountain forms will also be found to be limited to the mountains because their habitat is not represented on the lowland; and it may be added that two of the lowland forms, the semi-aquatic snakes *Thamnophis proximus* and *Natrix sipedon transversa*, have been found only on the larger bodies of water, making it possible that lack of food in the small mountain streams excludes them from the mountains. While the explanation of the distribution of these snakes is only a suggestion, it is a logical one in the light of the behavior of the saxicolous forms. It can receive confirmation, however, only from experimental studies.

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[3] H. H. Newman and J. T. Patterson: Field Studies of the Behavior of Lizard *Sceloporus spinosus floridanus*, *Bull. Univ. Texas*, No. 137 (Sci. Ser. No. 15), Austin, 1909.

[4] A. G. Ruthven: An Interpretation of the Distribution of the Reptiles in Maggie Basin, Nevada, *Bull. Amer. Geogr. Soc.*, Vol. 47, 1915, pp. 948–952.

Exception will also probably not be taken to the general statement that habits and habitats may control distribution. Thus Bailey[5] has stated that "In eastern Texas many species stop short of filling the whole humid area, and when their ranges are carefully mapped are found to be absent from, or in fewer cases to be restricted to, some of the following nonforested sections: the Grand and Black prairies of the Fort Worth and Dallas region; the coast prairie; coast marshes; islands and beaches." But it has been argued that such ecological data apply to local differences in distribution and that the differences in the environments are not those which prevail over a sufficiently large area to affect the whole range of a species. This is likely to be true, but if the facts are sufficient to show that such zonal distribution as occurs on mountains may not be due to climatic factors they certainly weaken the general theory to this extent.

Comparison of Phytogeographic and Faunal Divisions

There is, moreover, a larger aspect of the problem to be considered. If the distribution of the species of particular genera of land animals is examined, it is clear that the ranges are more liable to be affected at the place of contact of vegetation regions than on boundaries of life zones. Phytogeographers recognize divisions of the flora of North America which do not harmonize with life zones but more nearly correspond to physiographic regions.[6] It is believed to be significant that the species and subspecies of many genera of animals with terrestrial habits are apparently associated with these divisions, or, to express the facts more correctly, the forms of a genus frequently respond to the changes in conditions at the boundaries of vegetation regions by not going beyond them without change. It is not evident that comprehensive faunal divisions can be recognized on this basis, but it is apparent from the monographic revisions of genera which have been published that the boundaries of the vegetation regions are critical areas affecting a considerable number of forms. This would be expected on the theory that several factors may control distribution for, since there are a number of changes in the environments at these points, a larger number of species is affected than would be the case if only one factor were changed. If this explanation is true it would indicate that detailed studies of environmental conditions over large areas and of the physiology of the organisms dwelling therein will show that, as on mountains, the variation in any factor may control distribution and that the more numerous the factors which are changed the greater will be the number of species affected.

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[5] *Op. cit.*, p. 18.

[6] Compare the map of vegetation areas of the United States by Forrest Shreve, *Geogr. Rev.*, Vol. 3, 1917, opp. p. 124.

Physiological Ecology in Relation to Distributional Study

Physiological ecology is an aspect of zoölogy which has but recently come to receive the attention it deserves. As the study of the physiological relations existing between organisms and their environments, its data will provide a basis for the interpretation of the factors of distribution, and for the most part this interpretation must await the accumulation of ecological data. For this reason it is not possible, at present, as has been said, to prove that climatic factors are not the operative ones in controlling the distribution of forms which are confined to a particular region. However, since the effect of the inorganic contacts is largely physiological, we may well be guided by physiological facts in drafting our theories concerning the geographic factors and their operation. Physiologists have shown clearly that while temperature is an important physiological agent there are many other agents any one of which may be unfavorable at certain intensities. In other words, each environmental factor has an optimum intensity and unfavorably affects the animal at intensities either above or below the optimum.

Furthermore, it has been established that there are great physiological differences between species, both the optimum intensity of agents and the range of tolerance being characteristic for different forms. It is not necessary to illustrate these general physiological principles, but it is to be understood that the life-zone theory—that particular intensities of climatic factors exert a controlling influence on the distribution of many forms—is based on the assumption that many animals, or at least many terrestrial vertebrates, are physiologically similar in one respect, whereas there is no supporting physiological evidence for this assumption. If temperature changed suddenly and so radically as to surpass the range of tolerance of a large number of animals the life-zone theory would be more logical, but climatic variations are as a rule gradual.

Environmental Relations a Complex

From the ecological and physiological viewpoint it is necessary to consider the environment as a complex "the sum of all the contacts which an organism or a group of organisms establishes with the forces and matter of its surroundings, either organic or inorganic."[7] If the environmental relations of an animal are a complex it must follow that the variation of any feature of the environment may alter the whole in a way disastrous to the existence of the form and may cause extinction or function as a barrier to migration or ecesis. This conception of the nature of the environmental relation together with the physiological diversity of animals negatives the expectation that any one factor will ever be found to account for the present distribution of a fauna. The apparent zones become in reality only the habitats of a limited number of forms.

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[7] E. C. Case: The Environment of Vertebrate Life in the Late Paleozoic in North America: A Paleogeographic Study, *Carnegie Instn. Publ. No. 283*, Washington, D. C., 1919, p. 40.

It is possible that changes in temperature and moisture, either directly or through effects on the flora, are the factors which most often change the environments sufficiently to control the north-and-south and the east-and-west distribution of forms on great continents like North America, but this remains to be proved. Furthermore it is not evident that the considerable number of physiologically different forms composing the fauna responds to the same changes in the intensity of an environmental factor so as to permit of its division into zones. In ignoring the physiological and ecological data it is apparent that adherents of the life-zone theory are falling into the error of some anthropogeographers who, as Miss Semple has put it, "are prone to get a squint in their eye that makes them see one geographic factor to the exclusion of the rest; whereas it belongs to the very nature of physical environment to combine a whole group of influences, working all at the same time under the law of the resolution of forces."

In conclusion it may be pointed out that since the life-zone theory was first proposed the work of its advocates has largely been the listing of the faunas of the several zones and that nothing has been done to determine the effect of the assumed or other possible geographic factors. It needs to be understood that distribution cannot be explained by the mere mapping of the extent either of hypothetical faunal divisions or of species. The determination of the environmental factors is largely a physiological problem, and the data should be habits, habitat preference, analyses of conditions in the habitat, exact range, and the results of experiments upon the effect of altering the intensities of environmental factors.[8] Only harm can result from listing the forms by zones, for significant details of distribution are concealed, and the life-zone theory receives apparent but not real confirmation.

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[8] The classified list of ecological problems given by Barrington Moore (*Science*, No. 1307, Vol. 51, 1920, pp. 67–68), while incomplete, may be accepted by the student of zoögeography as a guide to the problems whose solution will throw light upon the environmental factors of distribution.